Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 125, No. 14

THE PROSCALOPINAE, A NEW SUBFAMILY OF TALPID INSECTIVORES

By Katherine M. Reed

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
November, 1961

No. 14 — *The Proscalopinae, a new Subfamily of Talpid Insectivores*

By Katherine M. Reed

INTRODUCTION

In the course of work on the insectivores of the Split Rock local fauna of Wyoming (Reed, 1960), I had an opportunity to examine the known material of *Proscalops* and its relatives. Matthew (1928, pp. 70-71) suggested in passing that the forms known to him might constitute a new family, although he considered this conjectural. With the discovery of at least three more of these highly distinctive forms since Matthew's time, the evidence now available indicates that at least a new subfamily of the Talpidae must be erected for the group.

I am indebted to the authorities of the American Museum of Natural History, the Chicago Natural History Museum, the Kansas University Museum of Paleontology, and Amherst College for the loan of specimens. Dr. Charles A. Reed, Dr. William Turnbull, Dr. Reid Macdonald, Dr. Paul O. McGrew and Dr. Raymond Alf all kindly assisted me with information about material in their collections. I also wish to thank Prof. Bryan Patterson and Mr. Craig C. Black for their help in this study, and the Mammal Department of the Museum of Comparative Zoology for access to Recent talpid and chrysochlorid material. I am also grateful to Prof. Harry B. Whittington for his assistance with the photography.

The following abbreviations are used:

A.C.M., Amherst College Museum; A.M.N.H., American Museum of Natural History; C.N.H.M., Chicago Natural History Museum; K.U.M.V.P., Kansas University Museum of Vertebrate Paleontology; M.C.Z., Museum of Comparative Zoology; l., length, antero-posterior; w., width, transverse; trig., trigonid; tal., talonid.

TAXONOMY

Family TALPIDAE

PROSCALOPINAE, subfam. nov.

Type genus. *Proscalops* Matthew, 1901.

Diagnosis. Skull chrysochlorid-like; dentition of talpid type.

Skull wide and deep in posterior part; flexure in maxillary, between P^3 and P^4, stronger than in *Neurotrichus;* lateral projections on premaxillaries; slight sagittal and occipital crests; palate long relative to skull length; antorbital rim confined to maxillary, not joining main body of zygoma. Wide lingual shelf on upper molars with hypocone varyingly developed; dental formula $I\frac{3}{?}$ $C\frac{1}{1}$ $P\frac{3}{?}$ $M\frac{3}{3}$.

Included genera. *Proscalops* Matthew, 1901; *Mesoscalops* Reed, 1960; *Oligoscalops* gen. nov.

Range. Mid-Oligocene to mid-Miocene, North America.

Only *Proscalops miocaenus* and *Mesoscalops scopelotemos* have hitherto been clearly diagnosed. Diagnoses of all species, in order of their chronologic appearance follow.

OLIGOSCALOPS gen. nov.

Type species. Oligoscalops whitmanensis sp. nov.

Range. Mid-Oligocene, Wyoming and Colorado.

Diagnosis. Roots of P^3 partially divided, tooth laterally compressed, abutting against P^4; P^4 with large parastylar area and lingual cusp situated at mid-line; protocones of molars directed antero-internally; M^2 wider than long; metastyle of M^3 subparallel to line joining protocone and metacone; hypocone rudimentary.

OLIGOSCALOPS WHITMANENSIS sp. nov.

Type. C.N.H.M. no. P 25800, partial skull and jaws.

Hypodigm. Type and K.U.M.V.P. no. 8143, left ramus with P_2-M_3.

Horizon and locality. Mid-Oligocene, type from Brule fm., Whitman, Niobrara County, Wyoming, collected by Dr. Paul O. McGrew. K.U.M.V.P. no. 8143 from middle Cedar Creek member of White River fm., W 1/2 sec. 7, T 11 N, R 53 W, Logan County, Colorado, collected by Dr. Edwin C. Galbreath.

Diagnosis. As for the genus; the smallest known member of the Proscalopinae.

Measurements (in millimeters).
C.N.H.M. no. P 25800

M^1 left	l. 2.2	M^3 left	l. 1.4
	w. 1.7		w. 1.4
right	l. 2.1–	right	l. 1.4
	w. 1.65		w. —
M^2 left	l. 1.7	M_2 right	l. 1.95
	w. 2.0		w. trig. 1.35
right	l. 1.8		w. tal. 1.35
	w. 2.1		

Skull width at M^2: 9.0
K.U.M.V.P. no. 8143

M1 left	l.–	M_3 left	l. 1.5
	w. tal. 1.0		w. trig. 1.3
M_2 left	l. 2.1		w. tal. 0.9
	w. trig. 1.7		
	w. tal. 2.1		

Proscalops Matthew

Type species. Proscalops miocaenus Matthew.

Range. Late Mid-Oligocene to early Miocene.

Emended diagnosis. Lateral premaxillary projections dorsoventrally compressed; diastema between P^3 and P^4; P^3 small, oval, single rooted; P^4 lacking parastylar area with lingual cusp anterior to mid-line; upper molars with or without well developed hypocones; parastyles incipient on M^1, definite on M^2.

Proscalops miocaenus Matthew

Matthew, 1901, pp. 375-376, figs. 1-2; 1909, pl. 49, fig. 5; Galbreath, 1953, p. 49.
2 MCZ (Reed 6007 Mre7 Aug7

Type. A.M.N.H. no. 8949a, broken skull and jaw.

Hypodigm. Type only.

Horizon and locality. Mid-Oligocene, Vista beds, Cedar Creek, Logan County, Colorado, collected by Dr. W. D. Matthew.

Emended diagnosis. Smallest known species of the genus. P^4 relatively narrower than in *Proscalops tertius*, lingual cusp directed posteriorly; lingual portions of upper molars narrower than in other species of the genus, with hypocones and protostyles less developed. M^3 compressed antero-posteriorly, lingual portion narrow, hypocone rudimentary.

Measurements (in millimeters).
A.M.N.H. no. 8949a

P^4 left l. 2.0		M^2 right l. 2.2	
w. 1.7		w. 2.7	
right l. 2.0		M^3 right l. 1.5	
w. 1.8		w. 1.8	
M^1 right l. 2.8			
w. 2.5			

Palatal width at M^2: 9.4 (from Matthew, 1901, p. 376).

Proscalops tertius sp. nov.

Type. A.M.N.H. no. 19420, partial skull and left ramus with M_{1-3}.

Hypodigm. Type only.

Horizon and locality. Oligocene, "White River fm.," possibly Brule, "Badlands, South Dakota," collected by Dr. G. L. Jepsen. No more precise information is available.

Diagnosis. Teeth very slightly larger and hypocones better developed than in *Proscalops secundus;* lingual cusp of P^4 essentially conical, larger than in *P. miocaenus*, no part extending anterior to labial cusp; metaconid of M_2 with minute metastylid, wide opening of talonid valley to interior as in *Mogera wogura.*

Measurements (in millimeters).
A.M.N.H. no. 19420

P^4 left l. 2.1	M^3 left l. 2.4
w. 2.1	w. —
right l. 2.1	right l. 2.1
w. 2.2	w. 2.1
M^1 left l. 3.2	M_1 left l. 2.85
w. 2.7	w. trig. 1.6
right l. 3.2	w. tal. 2.05
w. 2.8	M_2 left l. 2.7
M^2 left l. 2.8	w. trig. 1.8
w. 2.65	w. tal. 2.1
right l. 2.9	M_3 left l. 2.2
w. 2.75	w. trig. 1.6
	w. tal. 1.3

Skull width at M^2: 12.0

Proscalops secundus Matthew

Matthew, 1909, p. 559, pl. 51, figs. 3, 4; Galbreath 1953, p. 49.

This species has never been formally described or diagnosed. As Galbreath points out (1953, p. 49, footnote) "the type designation and specific name must be cited as figures 3 and 4 of plate 51, and the accompanying legends on page 559 of 'The Carnivora and Insectivora of the Bridger Basin Middle Eocene' (Matthew, W. D., 1909, Am. Mus. Nat. Hist. Mem., vol. 9, pt. 6)."

Type. A.M.N.H. no. 13798.

Hypodigm. Type only.

Horizon and locality. Early Miocene, "lower Rosebud" of Matthew, Bear-in-the-lodge Creek, South Dakota, collected by Dr. W. D. Matthew.[1]

Emended diagnosis. Larger than *P. miocaenus;* lingual cusp of P^4 broader and extending farther anteriorly than in *P. miocaenus*, about as in *Mesoscalops scopelotemos;* lingual portion of M^{1-3} broader, and hypocones better developed on M^{1-2} than in *P. miocaenus;* posterior root of zygomatic arch joining flange extending up side of cranium.

Measurements (in millimeters).

A.M.N.H. no. 13798

P^4	left	l. 1.85		
		w. l. 1.6		
	right	l. 1.9		
		w. 1.6		
M^1	left	l. 3.1		
		w. 2.6		
	right	l. 2.7		
		w. 2.5		
M^2	left	l. 2.55		
		w. 2.8		
	right	l. 2.4		
		w. 2.8		
M^3	left	l. 2.3		
		w. 1.9		
	right	l. 2.2		
		w. 1.8		

Skull width at M^2: 10.7; skull is slightly crushed transversely.

Mesoscalops Reed

Type species. Mesoscalops scopelotemos Reed 1960.

Range. Mid-Miocene, Wyoming.

Diagnosis. In general similar to *Proscalops*, but differing as follows: protocone of upper molars more rounded and somewhat larger than hypocone, situated more nearly directly internal to

[1] Macdonald (pers. comm.) suggests that the horizon may be either Monroe Creek formation or Harrison formation.

paracone, imparting a square appearance to the outline of teeth; P^4 with lingual face faintly grooved and with wide lingual shelf; lower molars with small median cingulum just above gum line between hypo- and protoconids, talonid of M_1 wider than trigonid.

Mescoscalops scopelotemos Reed

Reed, 1960, pp. 2-4, 7-8, pl. 1, pl. 2, figs. 1, 2.

Type. A.C.M. no. 10461, isolated left M^1.

Hypodigm. Type and numerous isolated teeth including P^4-M^3, M_{1-3}. (See Reed 1960, p. 2).

Horizon and locality. Mid-Miocene; NW 1/4 sec. 36, T 29 N, R 90 W, Fremont County, Wyoming, from the vicinity of the *Brachyerus* quarry seven miles west of Muddy Gap filling station, in a draw about 1/4 mile south of U.S. highway 287.

Diagnosis. As for the genus.

Measurements. See Reed 1960, pp. 7-8.

MORPHOLOGY

The subfamily Proscalopinae is at present represented only by skulls and partial rami or by isolated teeth. Leaving aside for the moment the possible but questionable association of *Arctoryctes-Cryptoryctes* with these forms, there are no postcranial elements known to me that can definitely be assigned to the species.

The skull

No sutures can be detected in any of the specimens, a situation not uncommon among small fossorial forms. The anterior portion of the skull is preserved only in *Proscalops secundus* and *Oligoscalops whitmanensis.* The two are similar in having lateral projections on the premaxillaries. In *Oligoscalops* these projections are abraded and now extend to a point above the roots of I^1; it is unlikely that they extended farther forward. The lateral projections are only faintly demarcated from the dorsal surface of the snout; a slight groove partially separates the nasals and the projections posteriorly. The lateral projections in *P. secundus* are more distinct than in the earlier form. As preserved, they extend slightly beyond I^1. The processes form conspicuous projecting shelves, flat dorsally, situated well below the level of the nasals. The edges of the projections tip upward very slightly. These projections are distinctly different from any structures in the same area in other talpids. There are slight dorsal swellings in the premaxillaries of the various talpids examined — *Scapanus, Parascalops, Talpa, Neurotrichus, Condylura, Scalopus, Mogera, Uropsilus, Desmana, Galemys, Rhynconax* — but in no case would these swellings significantly change the round or squarish outline of a transverse section through the anterior part of the skull. A similar section through either of the fossil skulls would give an elliptical section with the major axis horizontal. The projections are more nearly comparable to the premaxillary projections of the chrysochlorids, but here too there are distinct differences. The narial opening of the Proscalopinae is situated immediately above the incisors with no antero-dorsally inclined bony shelf above I^1, such as occurs in the African chrysochlorids, especially in *Chlorotalpa*. In *Amblysomus* and *Eremitalpa* the lateral projections are on the same level as the nasals and tend to converge ventro-medially, rather than more medially as in the Proscalopinae. In all chrysochlorids the projections extend beyond the tooth-bearing portion of the premaxillary, and in none are the projections as distinctly differentiated from the general outline of the skull as they are in *P. secundus*. *Oligoscalops* more nearly resembles the chrysochlorids in this latter respect. In a specimen of *Eremitalpa* (M. C. Z. no. 39614), the cartilage of the rhinarium remains. The cartilage is attached to the premaxillaries ventrally and the nasals dorsally; it is supported ventro-laterally by the lateral projections. It is likely that the projections in the Proscalopinae served a similar purpose. The similarity in structure to the chrysochlorids thus suggests a nasal region more chrysochlorid-like than mole-like.

On the skull of *Oligoscalops* there are two slight depressions above I^3, one on either side. These are on the dorsal side of the premaxillary and are slightly deeper antero-medially than posteriorly. Analogous depressions are not immediately evident on *P. secundus*, but may be represented by the dorsal surface of the lateral projections and possibly the vertical portions of the premaxillary medial to the projections. Nothing similar occurs either in talpids or in chrysochlorids.

When the skulls of *Proscalops secundus, Oligoscalops whitmanensis*, and *Proscalops tertius* are viewed in profile, a feature common to all can be seen, namely, a notable difference in the depth anteriorly and posteriorly. This difference can be measured only in *P. secundus* and *tertius*, where the cranial region is reasonably complete, but a similar difference is clearly suggested in *Oligoscalops*. The difference between the two dimensions is above or at the upper limit of similar measurements in both talpids and chrysochlorids.

The tooth row in the Proscalopinae shows a flexure or arching between P^3 and P^4, even more pronounced than in *Neurotrichus*. Anterior to P^4, the tooth row tends to parallel the dorsal profile of the antorbital portion of the skull. Posterior to P^4 the tooth row and the skull profile diverge, the tooth row descending. This characteristic can be seen in all the skulls, even in that of the poorly preserved *P. miocaenus;* it is best shown by *P. secundus*. This flexure occurs at the shallowest part of the skull. A similar flexure cannot be found in other talpids except *Neurotrichus*, or in the chrysochlorids.

The structure of the zygomatic arch distinguishes the Proscalopinae both from other talpids and from the chrysochlorids. The anterior part of the zygoma is preserved in all the available skulls. The anterior part of the arch in all is slender and rounded, stouter than in Recent talpids, but not as deep as in the chrysochlorids. The entire arch is preserved on the left side of *P. miocaenus;* it maintains its diameter throughout as in modern talpids, the cross-section of the posterior root being essentially the same as that of the anterior. In *P. tertius*, the left side of the skull preserves a small rounded posterior root; the right side corresponds, although badly worn. *P. secundus* likewise preserves a small rounded posterior root. This is a notable difference from chrysochlorids in which the arch increases greatly in depth posteriorly. The arch in the fossil forms shows no upward bending as in *Uropsilus* or *Rhynconax*. The facial regions of *P. secundus*, *P. tertius* and *Oligoscalops* are widest at the level of M^2. The zygomatic arch leaves the side of the facial region above the posterior margin of M^2, as in *Scapanus californicus* and *Uropsilus*. In all other talpids, the arch leaves opposite M^3 or the posterior margin of the tooth row. In chrysochlorids the arch begins above M^2, except in *Eremitalpa*. The antorbital border, which, due to the size of the infra-orbital foramen, forms a bar as in other insectivores, does not reach to the zygoma but joins the main body of the maxillary medial to the zygoma. The bar has a very slight posterior slant to it. This feature of the skull is in decided contrast to the Talpinae, Condylurinae and Scalopinae and to the chrysochlorids in which not only does the bar join the zygoma, but it also has a distinct posterior slant, uniting with the arch posterior to the tooth row. In *Mogera*, the bar appears to be attached to the side of the facial region, but here the posterior slant is greater than in the Proscalopinae. In *Uropsilus*, however, the bar is stout, posterior to the infraorbital and the large lacrymal foramina and joins the maxillary. It does not make up any part of the zygoma. The bar in *Desmana* joins medial to the rim of the zygoma, but is not attached to the maxillary.

In *P. secundus*, there is evidence of a squamosal flange extending up the side of the skull, suggestive of the chrysochlorid condition. However, the zygoma plays no part in the formation of the flange in *P. secundus* as it does in the chrysochlorids. It is impossible to determine the original width due to breakage. Matthew's figure (1909) shows that some of this flange has been lost since the photograph was made. The dorsal part of the flange is lacking, but it is probable that it extended to the slight sagittal crest present in this form. At a point approximately one-third of the distance between the glenoid fossa and the sagittal crest there is a buttress that divides the depression made by the flange into two portions, the ventral evidently deeper than the dorsal. A somewhat similar buttress is found in *Amblysomus* and *Eremitalpa* at the point where the flange joins the side wall of the cranium. However, the flange in *P. secundus* undoubtedly did not end at the buttress but continued toward the sagittal crest becoming progressively shallower dorsally. It is probable that the squamosal in this form resembled that of the large chrysochlorid, *Chrysospalax*, rather than the smaller forms, in the degree of projection from the skull, as shown in Matthew's figure. *Desmana*, which has both a sagittal crest and lateral, nearly horizontal flanges at the extremities of the occipital crest, does not in the least resemble *P. secundus* in this region.

The occipital region of the *Proscalopinae*, best seen in *P. secundus*, shows some resemblance to both talpids and chrysochlorids. The fossil skull preserves a trace of the occipital crest found in Recent talpids, especially prominent in *Desmana*. This crest is not found in the chrysochlorids; instead there is a crest which follows, essentially, the fronto-parietal suture above and the junction of the squamosal and the posterior part of the zygoma below. This crest is also present in the Proscalopinae.

The palate in the Proscalopinae extends posteriorly to a line joining the posterior borders of M^3, as in *Neurotrichus*. This character easily distinguishes the Proscalopinae from *Talpa*, *Mogera*, *Uropsilus*, *Desmana* and *Scalopus*, in which the palate ends well posterior to M^3, or from *Condylura* in which the palate ends anterior to M^3. The chrysochlorids resemble *Talpa*, etc., in this respect. The incisive foramen in *P. secundus* and *Oligoscalops* is situated immediately medial to a point between I^{1-2}. The incisive foramen is more posterior in chrysochlorids. The posterior palatal foramina can be seen in *P. secundus* and *Oligoscalops*; they occur on a line joining the postero-labial roots of the first molars. There are no palatal vacuities. Although neither the skull of *P. secundus* nor that of *Oligoscalops* is complete or free from distortion, it is obvious on inspection that the palate is longer relative to the total skull length and to basicranial length than in Recent talpids or in chrysochlorids (Table I).

TABLE I

Genus	Length of palate in cm.	Length of basicranium in cm.	Basicranium/Palate
Proscalops secundus	1.54	1.23	.79
Oligoscalops whitmanensis	1.14	1.0	.88
Scapanus	1.53	2.1	1.3
Scalopus	1.43	1.69	1.17
Condylura	1.32	1.95	1.4
Mogera	1.59	2.44	1.4
Neurotrichus	1.0	1.23	1.2
Parascalops	1.38	1.79	1.3
Talpa	1.33	1.96	1.4
Uropsilus	1.0	1.14	1.14
Desmana	3.20	2.56	1.25
Chrysospalax	1.74	1.67	.96–
Amblysomus	1.22	1.23	1.00
Eremitalpa	0.87	1.0	1.1
Chlorotalpa	0.86	1.23	1.4

The condylar region of most Recent talpids easily distinguishes them from the Proscalopinae. With the exception of *Mogera*, the condyle is neither as stout nor as ventrally inclined a structure as in the fossil forms. Recent talpids also possess a small depression at the anterior end of the condyle, a feature not seen in the Proscalopinae. Chrysochlorids resemble the Proscalopinae in the structures of this region. The foramen magnum in Recent talpids has a notable nick that extends anteriorly to the level of the posterior lacerate foramen or even slightly anterior to it. The corresponding nick in the Proscalopinae extends to a similar position but is much less pronounced, due to the more ventral position of the condyle. The same is true of the chrysochlorids. The condylar and posterior lacerate foramina in the Proscalopinae are situated close to the condyle; the former is a narrow slit just above the articular area of the condyle. The position of these foramina is similar to that in Recent talpids. The carotid foramen is closer and more nearly lateral to the condylar and posterior lacerate foramina in the fossils than in *Scalopus* and other Recent talpids, but is not greatly different in position from that of the chrysochlorids. The carotid artery seems to enter the posterior wall of the bulla as in the talpids. It is the most conspicuous foramen in the skull.

The bullae of *P. tertius* are irregularly quadrangular in outline and are neither as inflated as in the chrysochlorids nor as flattened as in Recent talpids. They bear rounded crests that run medially from the external auditory meatus, the anterior and posterior parts of the bullae sloping upwards from the crests. In *Oligoscalops* the bullae are less differentiated from the skull, and the crests are less salient. No sutures between the various elements of the bullae can be seen, but a basisphenoid component was certainly present. As in Recent talpids, the bullae merge anteriorly with the side walls of the posterior narial passage but, in contrast to most of them, the basisphenoid and elements anterior to it are little if at all inflated or cancellous in the Proscalopinae. The basicranium in this area bears a slight but notable median crest that runs forward to about the level of the Eustachian openings. A similar but smaller crest can be seen in *Scalopus*, and in *Desmana* this crest is slightly larger. The external auditory meatus in *P. tertius* is a large opening, larger than in *Scalopus*. It is broken in the other fossil specimens. The foramen ovale can be seen in *P. secundus* in the usual position. Its large size suggests that it also gave passage to the tendon of M. tensor tympani, as in the chrysochlorids and smaller moles. It may also have housed a vein. The limits of the foramen rotundum cannot be determined, but it is anterior to the foramen ovale and in the usual position. The Eustachian openings are rather large and oval shaped, directed almost immediately ventrally. The openings are larger than any observed in chrysochlorids. Placed slightly lateral and posterior to the external auditory meatus is the stylomastoid foramen, and postero-medial to it is the hyoidean vagina. The two are separated from the external auditory meatus by a low bar of bone. Conditions here are much as in the chrysochlorids. In Recent talpids, such as *Scalopus*, the openings are situated postero-lateral to the carotid foramen, not antero-lateral to it as in the fossils. The hyoidean vagina is much more pronounced than in the Recent forms. There are two other noticeable depressions on either side of the skulls, postero-lateral to the carotid foramen. One is almost directly posterior to the hyoidean vagina, the other posterior to this but more medial. The latter depression is somewhat elongate transversely. The function of these depressions is unknown.

The glenoid fossa of *P. secundus* and *P. tertius* is a much more pronounced structure than in Recent talpids. It is wider transversely and deeper, more as in chrysochlorids. It differs from these forms in having a prominent, anteriorly placed dorsal lip. The postglenoid foramen is extremely small and is situated high on the posterior face of the glenoid fossa near its lateral extremity. It is somewhat less lateral in position in the chrysochlorids, where it is on the medial face of the fossa and more nearly dorsal to the external auditory meatus. The usual condition in Recent talpids is for the foramen to be situated ventral to the posterior wall of the fossa, immediately dorsal to the anterior crus of the tympanic.

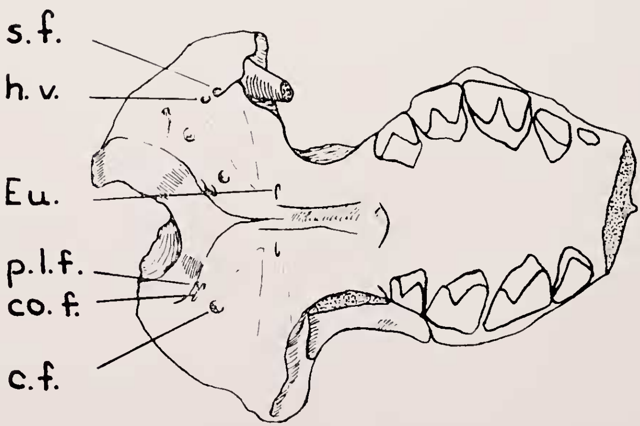

Fig. 1. Diagram of the basicranial region of *Proscalops tertius*. Stippled areas represent broken parts of skull. x3. Abbreviations: c.f., carotid foramen; co.f., condylar foramen; Eu., Eustachian opening; h.v., hyoidean vagina; p.l.f., posterior lacerate foramen; s.f., stylomastoid foramen.

The lower jaw

Rami are known in *Proscalops tertius*, *P. miocaenus* and *Oligoscalops*. These are slender and relatively uniform in depth. The rami of *Oligoscalops* show a slight bowing down below P_4-M_1, corresponding to the flexure in the upper tooth row. This bowing down is unlike anything seen in other talpids or in chrysochlorids. The symphysis was evidently elongate but weak. This is suggested by the rugose area on one of the rami of *Oligoscalops*, which extends posteriorly to P_4. In this respect the Proscalopinae do not differ from most talpids. The mental foramen, a single opening, is preserved only in *Oligoscalops*, where it is situated below P_3.

The posterior portion of the ramus is most completely preserved in *P. miocaenus* and the description is based on this specimen. The coronoid process rises at right angles to the main body of the ramus and, although incomplete at the tip, does not seem to curve posteriorly. It is not as narrow as in Recent talpids, and the posterior border, as in *Mogera*, has a forward slope. The condyle is wider than in Recent forms and is situated on a long stout neck. The angular process is short, stout and wide and leaves the body of the ramus at a lower level than in Recent talpids. In *Oligoscalops*, so far as can be told from the material, it is possible that the angle may have left the ramus at a somewhat higher level. The angle is not dorso-ventrally compressed as in *Uropsilus*. In comparison with the chrysochlorids, the proscalopine ramus is more slender. In the African forms, with the exception of the large *Chrysospalax*, the coronoid process is greatly reduced. The condyle is similar in inclination and in the structure of the neck, but the articular surface in the Proscalopinae faces essentially posteriorly whereas this surface in the chrysochlorids faces almost entirely dorsally. The angle of the chrysochlorids differs in being deeper and more compressed as well as projecting well below the horizontal ramus. The two groups are very distinct in this region.

The dentition

The diagnostic characters of the dentition of the members of the subfamily have been given in the taxonomic section. A more detailed treatment of the dentition and a brief comparison with Recent forms follow.

Upper dentition. In both *Oligoscalops* and *Proscalops secundus* the first incisor is enlarged and is flanked by two other small apparently conical incisors. I^3 is smaller than I^2 in *P. secondus;* these teeth are broken and represented only by the roots in

Oligoscalops. The canine is simple and conical in both specimens. It is larger than I^{2-3} in *P. secundus* and larger than the first premolar in *Oligoscalops*. All the incisors, canines and anterior premolars are separated from each other by diastemata. The premolar series consists of three teeth,[2] interpreted as $P^{1, 3-4}$. In *Oligoscalops*, P^3 is laterally compressed, has a partially divided root, and is in contact with P^4. In *P. miocaenus* the two anterior premolars are badly worn. P^3 is not laterally compressed as in *Oligoscalops* and has one root. A diastema separates P^3 and P^4 in all species of *Proscalops*. In *P. secundus*, $P^{1, 3}$ are simple, conical and single-rooted teeth. P^3 is present on the left side of *P. tertius* and agrees in form with that of *P. secundus*. These teeth are not known in *Mesoscalops*.

P^4 differs in the several species. In *Oligoscalops*, although worn, it consists of a large labial paracone with a parastylar area and a small conical lingual cusp. The latter cusp has a slightly pinched appearance and is directed posteriorly. In all the species of *Proscalops* and in *Mesoscalops*, P^4 lacks the parastylar area. In *P. miocaenus*, both the tooth as a whole and the lingual cusp are relatively larger than in *Oligoscalops*; again, the lingual cusp is directed posteriorly. P^4 of *P. tertius* is larger still and also has the essentially conical lingual cusp directed posteriorly. A change in P^4 becomes evident in *P. secundus*. In this species the lingual cusp has broadened and is more shelf-like in shape. It is also directed more medially than posteriorly, although no part of the lingual cusp extends anterior to the blade-like paracone. In *Mesoscalops* the antero-posterior broadening of the lingual cusp is carried further; it is here distinctly shelf-like. The lingual cusp extends slightly anterior to the paracone, although still directed essentially medially; it shows a partial division and the margin bears irregularities in the form of swellings. These are also present but are less numerous in *P. secundus*. One specimen of *Mesoscalops* exhibits a small cuspule on the posterior side of the labial cusp. In *Oligoscalops* and the species of *Proscalops* the tooth has three roots, two labial and one lingual. In *Mesoscalops* the roots have fused, but traces of the original divisions remain.

M^1 in *Oligoscalops* is triangular in general outline, with the protocone directed anteriorly. The hypocone is rudimentary, a mere protuberance labial and posterior to the protocone. The blade-like paracone is smaller than the V-shaped metacone. In *P. miocaenus* the tooth is generally similar, although the hypocone is somewhat better developed and the lingual portion of

[2] The premolar series might be $P^{1-2, 4}$ by analogy with *Uropsilus*.

the tooth therefore somewhat broader. A rudimentary protostyle is present. Para- and metacones are similar to those of *Oligoscalops*. In *P. tertius* the hypocone is well developed. There is a small but distinct protostyle anterior to the protocone, and a minute hypostyle posterior to the hypocone. The protocone is directed somewhat more medially than in the earlier forms. The paracone is again smaller and more blade-like than the metacone. *P. secundus* continues the trend toward a squaring up of the outline of the tooth. The lingual shelf is wider, and the hypocone and protostyle better developed. The paracone is slightly more V-shaped than in earlier forms, and there is a small distinct parastyle. A metastyle is also present. M^1 of *Mesoscalops* has the protocone and hypocone more nearly equal in size, and lacks a protostyle, which gives a distinctly square appearance to the tooth. The para- and metacones resemble those of *P. tertius*, rather than those of *P. secundus*. Both the parastyles and metastyles are present.

M^2 of *Oligoscalops* and *P. miocaenus* are again similar, although that of the latter is larger and has a more pronounced protocone and parastyle; a metastyle is lacking. In both, the paracone and metacone are V-shaped. *P. tertius* is similar in general, again enlarging the lingual portion of the tooth by a well developed hypocone. It also has a parastyle, but no distinct metastyle. The tooth is essentially square, with paracones and metacones subequal in size. *P. secundus* is very similar, possessing a slightly more distinct parastyle and a rudimentary metastyle. In *Mesoscalops* the protostyle is less distinct, due to the equalization of the protocone and hypocone. A parastyle is present, but the metastyle is incorporated in the crest from the metacone.

M^3 in *Oligoscalops* and *P. miocaenus* is distinctly triangular, with the protocone directly lingual to the paracone. The hypocone is rudimentary in *Oligoscalops*, absent in *P. miocaenus*. There are no distinct stylar cusps in either form. This tooth, in both, is antero-posteriorly compressed, slightly less so in *Oligoscalops*. The posterior margin of the tooth is formed by the blade-like metacone. M^3 of *P. tertius* is similar although larger. The hypocone, however, is clearly present and lingual to the metacone which again forms the posterior margin of the tooth. A protostyle is suggested by a slight swelling. *P. secundus* has a wider lingual area with a distinct hypocone and protostyle. The metacone still forms the posterior margin of the tooth, although on RM^3 there is a minute cuspule posterior to the metacone. A parastyle is present but there is no distinct metastyle. In *Mesoscalops* the hypocone is small and rather variable in shape, and the protostyle is very poorly developed. No distinct stylar cusps are seen. In all the specimens, M^3 is the smallest of the molars.

All the upper molars have three roots, two labial and one lingual. In *Mesoscalops* the lingual root is stouter and longer than the labial roots. The same is suggested for the others. In all, the protocone acquires a decidedly pinched appearance with wear, but the degree of pinching is not diagnostic.

Lower dentition. The incisors, canines and anterior premolars in *Oligoscalops*, the only form in which these teeth are known, are all broken or badly worn. The Kansas specimen suggests that the canine and P_1 and P_3 were simple, conical and single rooted. P_4 is laterally compressed and two rooted. In M_1 the talonid is wider than the trigonid, judging from the fragments that remain, and the opposite is true of M_2. A small anterior cuspule is preserved at the base of the paraconid of RM_2. In M_3 the trigonid is wider than the talonid. The relative sizes of the cusps on the molars cannot be determined, due to breakage. Matthew (1909, pl. 49) figures a right ramus of the type of *P. miocaenus*[3] in which the relative trigonid-talonid widths are as in *Oligoscalops*. The metaconid of M_2 is larger than either the paraconid or the entoconid. An anterior lingual basal cuspule is present in M_3. P_4 of this specimen has a small heel, but is essentially conical and apparently two rooted. P_3 is simple, conical and single rooted. All the left lower molars of *P. tertius* are known. In M_1 the trigonid is narrower than the talonid. The paraconid and metaconid diverge more than in M^{2-3}, and a small posterior cingular cuspule and a slight swelling on the lingual face of the paraconid are preserved. In M_2 the trigonid is wider than the talonid. The metaconid is stout with a rudimentary metastylid; there are both antero-internal and postero-internal cuspules. In M_3 the trigonid is again wider than the talonid. There is only an antero-internal cuspule. The lower dentition of *P. secundus* is unknown. M_1 of *Mesoscalops* has the trigonid narrower than the talonid, with the paraconid and metaconid widely divergent. A small postero-internal cuspule is present. M_2 has a metastylid, even more distinct than that in *P. tertius*, as well as antero-internal and postero-internal cuspules. The trigonid is equal in width to the talonid. M_3 has a simple metaconid and both antero- and postero-internal cuspules. The trigonid is wider than the talonid.

[3] This part of the type was not included in the material sent to me for study.

Comparison with Recent forms

Although the teeth of the Proscalopinae are talpid-like, a brief comparison with Recent forms is desirable. Most of the Recent talpids have three incisors, the first enlarged, the second and third decreasing in size. *Condylura*, however, has a large caniniform second incisor, larger than either I^1 or the canine. *Uropsilus*, apparently with only two incisors, possesses an enlarged I^2, but it is lower than I^1. In *Scalopus* the second and third incisors are minute and placed very close together. The second incisor is separated from the very large I^1 by a large diastema in *Desmana*. The canines in all but *Talpa* and *Mogera*, where they are large, are only slightly larger than the second or third incisor or the first premolar, as in the Proscalopinae. *Scalopus* and *Condylura* are the only Recent forms with a reduced premolar series. In *Uropsilus* P^3 is either present or absent; where present it is greatly reduced.[4] P^2 in this form is larger than both P^1 and P^3. P^4 shows the greatest difference between the Recent and fossil forms. *Condylura*, *Parascalops*, *Mogera*, *Neurotrichus*, and *Talpa* all have a small basal cusp anterior to the paracone. The lingual cusp in these forms is extremely small. The general structure of P^4 of *Oligoscalops* shows some similarity to these five genera. Both the anterior basal cusp and the lingual cusp are essentially lacking in *Scapanus* and *Scalopus*. P^4 of *Uropsilus* is more similar to most of the Proscalopinae than other talpids, but has a slight anterior cingulum not unlike *Desmana*. The lingual portion of the molars is narrower and lacks the hypocone development of the later Proscalopinae in all except *Neurotrichus*, *Parascalops*, *Uropsilus* and the members of the Desmaninae. In these forms the wider lingual portion does not show any pinching of the protocone, and the paracone and metacone of M^1 in *Neurotrichus* are much simpler than in the fossils. The position of the protostyle in *Desmana* is very different than in the Proscalopinae. In all Recent talpids, excepting *Scalopus* in which they are essentially lacking, the stylar cusps are more distinct than in the fossils. In the lower dentition, *Talpa*, *Mogera*, and *Condylura* have two-rooted premolar teeth. *Parascalops* and *Condylura* are the only Recent talpids that have metastylids on the molars. Although antero- and postero-internal cuspules are generally present, in no case do they connect with cingula as in the Proscalopinae.

[4] In three of four specimens examined, P^3 was present, although it was most greatly reduced in a male skull. The one skull lacking P^3 was also a male. Cabrera's dental formula is thus incorrect and should read for the upper dentition either I^2 C^1 P^4 M^3 or I^3 C^1 P^3 M^3, not I^2 C^1 P^3 M^3 as given (Cabrera, 1925, Genera Mammalium, vol. 2, Insectivora, Galeopithecia).

Cingula are usually lacking, except in *Uropsilus* and some of the Desmaninae.

Further comparison between the Proscalopinae and Recent talpids in the dentition seems unnecessary; the extinct forms clearly differ from the living in various characters and combinations of characters. No comparison with the zalambdodont chrysochlorids is required.

Arctoryctes-Cryptoryctes and the Proscalopinae

It has been suggested by Matthew (1928) and by Schlaikjer (1933) that the humeri described as *Arctoryctes* may belong to the *Proscalops* group. This suggestion must now be considered.

Two points tend to support such an association. First, both skulls and humeri have talpid characters, yet neither are typically talpid. (The humeri, of course, are very different from those of the chrysochlorids.) Second, the published geologic and geographic ranges of the Proscalopinae and the *Arctoryctes* group overlap (see Table II).

Table II

	Oligocene			Miocene	
	Early	Middle	Late	Early	Middle
Cryptoryctes kayi	Montana				
Cryptoryctes sp.?	Colorado*				
Arctoryctes terrenus			S. Dakota		
Arctoryctes galbreathi		Montana Colorado			
Arctoryctes sp.?	Nebraska				Wyoming**
Oligoscalops whitmanensis		Wyoming Colorado			
Proscalops miocaenus			Colorado		
Proscalops tertius			S. Dakota†		
Proscalops secundus				S. Dakota	
Mesoscalops scopelotemos					Wyoming

* Recorded, but lost in the field.
** Species not identified. (Reed, C. A., pers. comm., 1961).
† Exact horizon uncertain.

A comparison of the skull length/humerus length ratio has been made for modern talpids, for a chrysochlorid, and for selected proscalopine skulls and arctoryctine humeri. In two cases, skull material and humeri are known from the same horizon and locality: *Oligoscalops whitmanensis* (K.U.M.V.P. no. 8143) and *Arctoryctes galbreathi* (K.U.M.V.P. nos. 9837-9839); and *Mesoscalops scopelotemos* and an unidentified species of *Arctoryctes*. In the first case, unfortunately, the two best preserved humeri are broken, and the measurements, kindly supplied by C. A. Reed, are only approximate. No measurements are available for the humeri found with *Mesoscalops scopelotemos*. There is a fair correspondence in time in one other case, that of *Proscalops secundus* and *Arctoryctes terrenus;* the former is probably from a somewhat earlier horizon in the Miocene of South Dakota than the latter. All other occurrences are rather widely separated in time or space. There is no known proscalopine that could correspond to the small *Cryptoryctes kayi*. The ratios (Table III) of *Oligoscalops whitmanensis*/*Arctoryctes galbreathi* and *Proscalops secundus*/*Arctoryctes terrenus* do not differ greatly from those of certain talpids but do differ from that of the only chrysochlorid available for comparison. These ratios at least suggest that association is not impossible.

TABLE III

specimen		skull/humerus ratio	remarks
Scapanus		229%	from Reed, 1954
Condylura		245%	" " "
Neurotrichus		304%	" " " (long skull)
Chrysochloris stuhlmani		180%	
Oligoscalops whitmanensis	skull	252-256%	based on estimated humeri lengths
Arctoryctes galbreathi	humerus		
Proscalops secundus	skull	245%	slight difference in age
Arctoryctes terrenus	humerus		

Although not impossible, the association of the skulls and humeri is, of course, very far from proven. A typical talpid humerus is known from the mid-Oligocene Cedar Creek member of Colorado (Galbreath 1953), the same deposit that has yielded specimens of *Oligoscalops whitmanensis* and *Arctoryctes galbreathi*. The earliest non-proscalopine North American talpid is *Domninoides;* two species of this genus are known from the earlier Miocene, one of them from beds just below those containing *Proscalops secundus* (Macdonald, pers. comm.). I have seen typical talpid humeri from a deposit that has yielded remains of *Domninoides* ("Valentine formation," Fort Niobrara locality) and strongly suspect that these humeri are referable to that genus. It seems likely that the Cedar Creek talpid humerus represents some otherwise unrecorded member of the family, but the possibility that it is referable to *Oligoscalops* should not be ignored — nor can the possibility be ignored that the *Arctoryctes-Cryptoryctes* humeri may be referable to some other group altogether. Only the fortunate discovery of proscalopine cranial or dental material in unmistakable association with arctoryctine humeri will settle the question.

After this study was completed, Russell (1960) suggested that the arctoryctine humeri may belong to *Micropternodus* and related forms, since a humerus, identified by C. A. Reed as *Cryptoryctes*, occurs at a locality that has yielded "*Kentrogomphios*" (= *Micropternodus*). Furthermore, if the skull proportions of *Micropternodus* are similar to those of talpids, the skull/humerus ratio of *Micropternodus* and *Cryptoryctes* (248%) is much closer to those of talpids than to those of epoicotherids or apternodontines, again suggesting a possible relationship between *Micropternodus* and *Cryptoryctes*.

This ratio is not very different from that obtained by comparing proscalopine skulls and arctoryctine humeri. However, as the evidence supporting the association of the humeri with either the Proscalopinae or the *Micropternodus* group is no more than circumstantial at best, it is not possible to draw any conclusions at this time.

CONCLUSIONS

The morphological characters of the skull obviously unite the proscalopine species and clearly separate them from other talpids. As regards intergroup relationships, it can be stated that *Oligoscalops*, the earliest known form, can be easily distinguished from the rest of the subfamily on the characters of P^3 and P^4, although the overall cusp pattern and the structure of the molars are not very different from *Proscalops*. Within the genus *Proscalops* there are certain trends in the evolution of the dentition that may easily be seen. There is a tendency to broaden the lingual portion of the upper molars and P^4, with a general squaring of the outline of these teeth. In the lower molars there is a progressive complication of the teeth by the addition of antero- and postero-internal cuspules and the development of a metastylid. *Mesoscalops*, the latest known form, while similar in the general pattern of the lower molars, has modified the upper molars by eliminating the protostyles. P^4 of this form differs in having incipient division of the lingual cusp as well as fusion of the roots. This genus could, however, have been derived from a form not unlike *P. secundus*. The mutual relationships within the subfamily appear to be as in Figure 2.

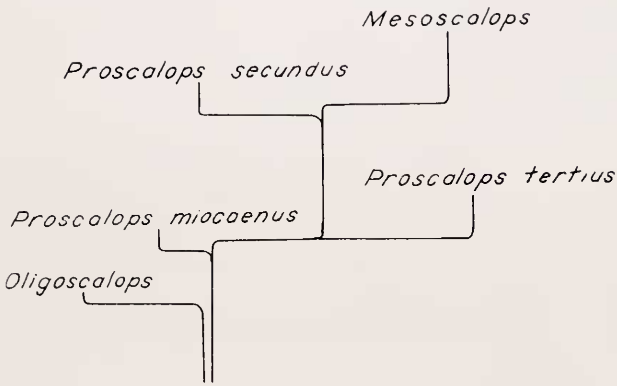

Fig. 2. Diagrammatic representation of the relationship of the known members of the Proscalopinae.

The Proscalopinae are very different from all other talpids so far as the characters of the skull are concerned. In this the group differs more from the other talpid subfamilies than these subfamilies do from each other. This suggests that it might be more proper to group all other moles, with the exception of the Desmaninae, in one subfamily. Our ignorance of the family is such, however, that I do not take this step. If the curious arctoryctine humeri should prove to be referable to the proscalopines, the combination of cranial and humeral characters would certainly warrant the erection of a new family for the Proscalopinae, as Matthew suspected.

It has been shown that there is a remarkable parallelism between the proscalopines and the chrysochlorids. This is particularly evident in the premaxillary region, the squamosal flange, seen particularly in *P. secundus*, and the general structure of the basicranial region. The fact that these peculiar fossorial adaptations have arisen more than once in the Insectivora removes some of the uniqueness of the chrysochlorids.

REFERENCES

CABRERA, A.

1925. Genera Mammalium. Vol. 2, Insectivora, Galeopithecia. Madrid, 232 p.

GALBREATH, E. C.

1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas, Paleontological Contributions, Vertebrata, Article 4, pp. 1-120.

HOUGH, J. AND R. M. ALF

1956. Chadronian mammalian fauna from Nebraska. Jour. Paleontology, vol. 30, pp. 132-140.

MATTHEW, W. D.

1901. Fossil mammals of the Tertiary of northeastern Colorado. Mem. Amer. Mus. Nat. Hist., vol. 1, pt. 7, pp. 355-447.

1909. The Carnivora and Insectivora of the Bridger Basin Middle Eocene. Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 6, pp. 291-567.

1928. *Xenotherium*, an edentate. Jour. Mammalogy, vol. 9, pp. 70-71.

REED, C. A.

1954. Some fossorial mammals from the Tertiary of western North America. Jour. Paleontology, vol. 28, pp. 102-111.

1956. A new species of the fossorial mammal *Arctoryctes* from the Oligocene of Colorado. Fieldiana, Geology, vol. 10, no. 24, pp. 305-311.

REED, K. M.

1960. Insectivora of the Middle Miocene Split Rock local fauna, Wyoming. Breviora, Mus. Comp. Zool., no. 116, pp. 1-11.

RUSSELL, D. A.

1960. A review of the Oligocene insectivore *Micropternodus borealis*. Jour. Paleontology, vol. 34, no. 5, pp. 940-949.

SCHLAIKJER, E. M.

1933. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. I. A detailed study of the structure and relationships of a new zalambdodont insectivore from the Middle Oligocene. Bull. Mus. Comp. Zool. Harvard Coll., vol. 76, pp. 1-27.